Hormonal control of cambial activity and xylem differentiation in apple shoots

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INTRODUCTION

The knowledge of the factors controlling cambial activity and the differentiation of conducting tissues is not only important from the theoretical point of view but also for the success of common horticultural practices like grafting and budding. The purpose of our work was to elucidate the problem of cambial activity in apple shoots, and the differentiation of xylem components. The extensive review of the problem was presented in 1963 by Romberger, and in here due to shortage of space only the most pertinent and recent contributions are referred to in the discussion.

The studies on the effects of synthetic growth regulators such as auxins, cytokinins and gibberellins were enlarged to include some growth retardants in order to present more complete evidence on their role in cambial activity. The effects of those growth regulators on the metabolism of cell wall formation in newly formed wood, on the production of phloem and the activity of phellogen will be presented separately.

The following abbreviations were used in the text:

- BA — 6-benzyladenine
- GA — Gibrescol (Polfa, Poland) containing 92% of gibberellic acid
- NAA — naphthylacetic acid
- CCC — 2-chloroethyl trimethylammonium chloride
- B-9 — N-dimethyl amino succinamic acid.

MATERIAL AND METHODS

One-year-old 'Antonovka' seedlings and 4 year-old 'Antonovka' trees were used in the experiments. Growth regulators were supplied in water solution. The method of supplying the growth regulators used previously (Pieniążek 1964) was not quantitative due to the leakage of solution through rubber tubing. The method was improved by putting the cotton wick in the rubber or plastic

tubing which prevented the leakage and it gave us means of measuring the absorption of growth regulators by decapitated stem or petiole stump (Fig. 1, 2). The treatments and the experimental trees were as given below.

Fig. 1 and 2. The method of supplying growth regulators in solution to the decapitated stems and petiole stumps. (Explanations in the text).

A. Trees chilled outdoors

a. One-year-old seedlings were brought from the outside into a heated greenhouse (15° – 25°C) at the end of February 1967 and treated with growth regulators on March 3rd. The plants were decapitated and completely disbudded (with the exception of treatment 1) and then treated with growth regulators. The concentrations are given in mg/l.

1. Control left intact	12. CCC-1600 plus GA-50
2. Control - water only	13. CCC-400, 1600 plus NAA-20 plus BA-70
3. NAA - 20	14. CCC-400, 1600 plus NAA-20 plus GA-50
4. BA - 70	15. CCC-1600 plus BA-70 plus GA-50
5. GA - 50	16. B-9 (400, 1600)
6. NAA-20 plus BA-70	17. B-9 (1600) plus NAA-20
7. NAA-20 plus GA-50	18. B-9 (1600) plus BA-70
8. BA-70 plus GA-50	19. B-9 (1600) plus GA-50
9. CCC-400, 1600	20. B-9 (400, 1600) plus NAA-20 plus BA-70
10. CCC-1600 plus NAA-20	21. B-9 (400, 1600) plus NAA-20 plus GA-50
11. CCC-1600 plus BA-70	22. B-9 (1600) plus BA-70 plus GA-50

b. One-year-old seedlings were brought from the outside into a heated greenhouse (15° – 25° C) at the end of February 1967. After a month of active growth the new shoots were removed and the plants decapitated. The following treatments were given:

1. Control left intact	3. NAA-20
2. Control - water only	4. NAA-20 plus BA-70
5. NAA-20 plus GA-50	

c. 4-year-old 'Antonovka' trees grown in the orchard. The current year shoots were decapitated on July 20th 1967 and four buds removed below the point of decapitation. Treatments as in Exp. A, a:2-8.

B. Unchilled trees

a. Four-year-old 'Antonovka' trees. The potted trees were brought to the heated greenhouse at the beginning of October 1966. All leaves were removed. The trees remained fully dormant until March 17th 1967 when one-year-old shoots were decapitated. The buds were not removed. Treatments as in Exp. A, a:2-22.

b. One-year-old seedlings. Leaves removed in the nursery before the plants were brought to the heated greenhouse. The seedlings remained fully dormant. They were decapitated on December 12th, 1966, and one bud was removed below the point of decapitation, and then treated as follows:

1. Control - water only	5. NAA - 20 plus BA-70
2. NAA - 2.5, 5.0, 10, 20, 40	6. NAA-20 plus GA-50
3. BA - 8.75, 17, 35, 70	7. BA-70 plus GA-50
4. GA - 25, 50, 100, 200	8. NAA-20 plus BA-70 plus GA-50

c. One-year-old seedlings obtained in the greenhouse at the beginning of 1966. The extension growth was terminated but the seedlings kept their green leaves. The buds remained dormant until the plants were treated with growth regulators in January to March 1967, as follows:

1. Control - water only	3. BA-50
2. NAA-20	4. NAA-25 plus BA-25
5. NAA-25 plus GA-50	

3 ml of solution were given per decapitated shoot, and in the case when they were present 2 ml per one petiole stump was given, 3 petioles per seedling being treated.

The absorption of 3 ml of solution took from 3 to 6 days by decapitated one-year-old seedlings without leaves. The four-year-old trees both in the greenhouse (without leaves) and in the orchard (with leaves) absorbed the solution in about 10 hours. The absorption through the petiole stumps was always very fast (about 6 hours).

There were 5 to 7 trees or shoots per treatment. The shoots of the treated plants were collected 24 days after treatment and fixed in 70% ethanol. They

were sectioned then in the middle of the internode below the bud scar and at 3, 5, 10 and 15 cm below the place of treatment. Transverse, longitudinal tangential sections were made, and the newly formed xylem that could be easily separated from the old xylem was macerated separately in the mixture of Schultze. The tissues were macerated directly on the microscopic slide, the individual vessel components photographed in phase contrast, and cut out from the prints. The characteristic xylem components were then arranged on the sheet of paper and photographed once more. For comparison tangential longitudinal sections from the same treatments are shown.

Transverse sections after treatment with a mordant (Javelle's water) were stained with malachite green and saffranin.

RESULTS

The effect of growth regulators on bud development of unchilled trees confirmed our previous results (Pieniążek and Jankiewicz 1966; Pieniążek, Saniewski and Jankiewicz 1967). One-year-old unchilled seedlings (Exp. B, b) after decapitation produced a small rosette of leaves (Fig. 3) whereas older 4-year-old trees remained fully dormant (Exp. B. a). 4-year-old 'Antonovka' trees developed however more buds per shoot (3-4) after treatment with BA although the buds were spaced farther apart and the growth regulator had a longer way to reach them than in the 1-year-old seedlings.

NAA (2.5 - 40 mg/l) inhibited bud opening resulting after chilling or wounding. When supplied in the mixture with BA or GA its inhibitory influence on bud growth was evident at all the concentrations of NAA, and it caused the well visible thickening of the axis (Fig. 4). Older trees treated with the mixture of NAA and BA (20 plus 70 mg/l) opened after 14 days 1-2 buds per shoot. GA did not break the dormancy of the buds but it stimulated the elongation of those buds that were previously stimulated into growth by wound effect or BA (Fig. 4).

Cambial activity. Control trees chilled outdoors when brought to the heated greenhouse on March 1st had non-active cambium. After a week there the buds became swollen but no cambial activity was noticed even immediately below the bud. When small rosettes of leaves were formed 2-4 new layers of xylem were formed only immediately below the growing bud. After a month when the new shoots were about 8 cm long the new xylem increment consisted of about 8 new layers of normal wood (Fig. 5). At the time when all the new shoots were cut off and the plants decapitated (Exp. A, b:1) it can be seen that the cambial zone is very wide and irregular, and the new vessels and tracheids are in the process of differentiation (Fig. 5). After 24 days water treated control shows a very different picture (Fig. 6). The cambium appears as a narrow zone of regular, flat cells and the differentiation of the last layer of xylem components resembles a typical pre-dormant late wood type.

After treatment with NAA (Fig. 7) the cambium became active again but only a few rows of abnormal wood were formed. NAA plus BA or NAA plus GA (Fig. 8, 9) produced the same synergistic effects in cambial growth as observed

Fig. 3 and 4. The effect of growth regulators on bud development and the thickening of the axis.

in our previous experiments (Pieniążek, and Jankiewicz 1966a). After NAA plus BA several times wider ring (30 new layers) of new growth occurred than found in control trees but it was also abnormal.

In unchilled one-year-old seedlings (Exp. B, b:2) treated with different concentrations of NAA (2.5 to 40 mg/l) new growth increment was observed already after 14 days. The width of the new ring was not affected by the used concentrations of NAA, and the synergistic effect on cambial activity in the presence of BA or GA was the same as in previously described treatment.

Unchilled four-year-old trees (Exp. B, a) growing under the same conditions in the greenhouse produced essentially the same results after treatments with growth regulators. However, the effect of NAA on cambial activity was evident at a longer distance than in the seedlings (15 to 20 cm). The synergism between NAA plus BA and NAA plus GA was very marked (Figs 10, 11, 12) but NAA at 20 mg/l did not inhibit the bud growth as much as in the seedlings when supplied together with BA. In the trees treated with NAA plus BA the bud developed later than the newly formed xylem ring. Fig. 12 shows that the first abnormal increment was produced by NAA plus BA and the second of normally differentiated wood when the buds became active.

Essentially similar results were obtained with current year shoots of four-year-old 'Antonovka' trees grown in the orchard (Exp. A, c) and treated with growth regulators on July 20th. They displayed the same effects of growth regulators on the reactivation of cambial activity and new xylem differentiation as both chilled and unchilled trees.

The unchilled seedlings produced in the greenhouse (Exp. B, c) that have kept their leaves all year long behaved likewise when treated with growth regulators in January to March of the following year. However, the uptake of growth regulators through the petiole stumps was very rapid and the new growth ring produced after NAA treatment was found above the treated petiole stumps. After BA treatment many buds were stimulated into growth and some of the newly formed shoots were 8 cm long. The width of the new growth ring produced during 24 days was greater than in control chilled and intact plants (Fig. 19 and Fig. 5).

The growth retardants (Exp. A, a and Exp. B, a) - CCC and B-9 when applied separately or in combination with the other growth regulators failed to produce any changes in cambial activity and wood differentiation when supplied directly to the stem. B-9 at 400 mg/l like CCC at the same concentration did not affect cambial activity but at 1600 mg/l the shoots of the seedlings were killed in all the treatment with other growth regulators. In 4-year-old trees the retardants like in the seedlings exerted no influence on bud or cambial growth and no toxic effects were observed on the shoots.

Xylem differentiation. The newly formed xylem after the treatments with NAA, NAA plus BA and NAA plus GA was composed mainly of vessels and parenchymatous cells. Figs 13-18 show apple xylem on longitudinal tangential sections and after maceration. Normal xylem in control plants is composed

Fig. 5. A new xylem ring produced by control chilled plants after a month of growth in the greenhouse. The last layer of xylem with undifferentiated components. Magn. $\times 120$.

Figs 6, 7, 8. As above but the new shoots removed and the plants decapitated. The cambium after 24 days non-active and the last layer of xylem resembles pre-dormant late wood type. 7 and 8 - the plants treated with growth regulators: 7 - NAA-20 mg/l. Reactivated cambium produced a narrow ring of abnormal xylem; 8 - NAA-20 + GA-50 (mg/l). A wide ring of abnormal xylem.

Fig. 9. The plant treated with growth regulators: NAA-20 + BA-70 (mg/l). A wide ring of abnormal xylem.

Figs 10, 11, 12. The effect of growth regulators on unchilled 4-year-old trees: 10 - NAA-20 mg/l; 11 - NAA-20 + GA-50 (mg/l); 12 - NAA-20 + BA-70 (mg/l). Cambium produced abnormal xylem ring and then when buds became active normal wood was formed.

Figs 13 to 18. Longitudinal tangential sections of apple xylem (left) and xylem components after maceration (right): 13 - Control, Magn. $\times 560$; 15 - NAA-20 + BA-70 mg/l; 17 - NAA-20 + GA-50 mg/l; 14 - Control, Magn. $\times 290$; 16 - NAA-20 + BA-70 mg/l; 18 - NAA-20 + GA-50 mg/l.

Fig. 19. Unchilled one-year-old trees with old leaves. BA stimulated the dormant buds into growth and a wide, almost normal ring of xylem was formed. Magn. $\times 120$. Figs 20 to 22. The influence of growth regulators on the meristematic activity in cortical layer. (Magn. $\times 85$). 20 - control; 21 - NAA-20 + BA-70; 22 - NAA-20 + GA-50

of vessels, fiber-tracheids and parenchymatous cells. The vessels have mainly pitted secondary thickenings. The ratio of fiber-tracheids to vessels is always high.

In new wood produced under the influence of NAA, NAA plus BA and NAA plus GA mostly vessels were found and they were shorter and narrower than in control wood, mostly with scalariform or reticulate thickenings and few with pitted secondary thickenings. The fibertracheids were very few, and the number of vessels several times more numerous than other components. However, after NAA plus GA treatment (Fig. 18) the new xylem contains longer components than the wood from NAA plus BA treatment (Fig. 16).

The unchilled seedlings with old leaves after BA treatment produced new shoots and in the newly formed very wide ring all the components of normal xylem were present. It seems though that the ratio of vessels to other xylem components was higher in those plants than that found in the normal wood (Figs 19 and 5).

The growth regulators induced also changes in the cortical layer. Fig. 20, 21, 22 show that the thickening of the axis after NAA plus BA treatment was due not only to the cambial but also to the meristematic activity in the parenchyma of the cortical layer. After NAA plus GA treatment parenchymatous cells in the cortical layer were very little affected by this treatment.

DISCUSSION

Our discussion is limited for the time being to the reactivation of cambium and its connection with the differentiation of xylem only. As it was mentioned previously the effects of growth regulators on the metabolism of cell wall formation in new wood, on the production of phloem and the activity of phellogen are being currently studied.

In one of our previous papers (Pieniążek and Saniewski 1968) we proposed that cytokinins are the hormones responsible for bud opening in the apple trees, and the buds in turn are suppliers of auxins and gibberellins necessary for initiation and maintenance of cambial activity.

It is well known (Wareing 1951) that in diffuse-porous species leaf expansion generally precedes cambial reactivation. This reactivation in case of 'Antonovka' trees does not occur simultaneously over the circumference of the shoot but only immediately below the developing rosette of leaves. The stimulus to divide proceeds down the stem relatively slowly and a remarkable relationship exists between the size of leaves, the length of newly developed shoots and the amount of cambial increment. It was calculated that a new shoot had to be at least 3 cm long before the new growth ring of 2 to 4 layers was found around the circumference of the shoot (Pieniążek and Saniewski 1968).

The data of Tepper (1967) provide plausible explanation for the effect of cytokinins in bud stimulation based on very interesting evidence of mitotic reactivation of the terminal cambium of White Ash. The first appearance of mitotic figures in reactivating buds of 1-year-old ash seedlings is in the leaf primordia. Subsequently, mitotic activity in the leaves increases and when this occurs mitotic figures begin to appear in the cauline portions of the shoot. In the shoot the mitoses predominate in and near the procambium, and all this takes place at the time the bud is beginning to expand noticeably. Cambial reactivation also occurs in the upper sections at this time.

It is also known that cytokinins are synthesized in the roots and transported in the xylem stream (Kulaeva 1962; Kende 1964; Pieniżek and Jankiewicz 1965), thus the reactivation of mitotic activity in the leaf primordia of apple trees under the influence of synthetic cytokinin such as BA might explain stimulatory effect of natural cytokinins on bud opening. On the other hand BA failed to reactivate the secondary meristems such as cambium and phellogen in apple shoots (Pieniżek and Jankiewicz 1966a).

Auxins produced by the developing buds and leaves seem to play the key role in the reactivation of the cambium both in chilled and unchilled trees. In our experiments cambial reactivation coming from the buds could be replaced by synthetic NAA at various concentrations and the lowest (2.5 mg/l) produced the same effect as the highest of 40 mg/l. In the absence of developing shoots the cambium of chilled and unchilled trees after hormonal reactivation produced only abnormal xylem. However, the transport of NAA in chilled trees took place on a longer distance (Pieniżek and Saniewski 1968). Gouwentak (1965) put forward a hypothesis that synthetic indolylacetic acid promotes efficiently cambial activity only in non-dormant woody shoots. She implied that in trees the initiation of cambial activity is dependent upon the presence of both auxin and an active non-dormant condition of the cambium resulting from chilling. In our experiments with apple trees treated with growth regulators at various stages of growth and dormancy it was possible to obtain very high cambial activity without the effect of chilling. In this auxin seems to be the most important factor for the initiation of cambial activity, whereas cytokinins and gibberellins are exerting synergistic effect on the rate of cambial divisions and the differentiation of normal xylem components. Supporting evidence was obtained when NAA supplied to the disbudded chilled seedlings produced only a very narrow ring of abnormal wood at a short distance below the point of NAA application, whereas close to the base of the tree we were surprised to find a wide ring of normal xylem. It could be then said that the other limiting factors in xylem differentiation were provided in the xylem stream from the basal portion of tree i.e. from the roots where probably cytokinins and also gibberellins are synthesized (Kende 1964; Šebánek 1967). Dvořák (1961) also observed in peach trees after disbudding the formation of normal growth ring close to their base when in the apical part of the tree no new wood was detected.

A distinct difference exists between ring-porous and diffuse-porous species in the transmission of cambial stimulus after winter rest. Wareing (1951, 1958) speculated that the rapid spread of cambial activity in ring-porous species is due to the presence of a hormone precursor in the cambial or cortical tissue before bud break. Digby and Wareing (1966) have demonstrated a growth promoting substance in the cambium of ring-porous (*F. excelsior*) but not in diffuse-porous species. This substance has an R_f value which corresponds closely to the R_f of tryptophan. The authors suggested that the rapid conversion of tryptophan to indolyl-acetic acid is responsible for the rapid spread of cambial activity in ring-porous species.

In apple shoots auxin precursor, if exists, is not stored in sufficient amount after winter rest to initiate cambial activity in disbudded shoots. Even after a month of active growth when the shoots were about 8 to 12 cm long and quite wide ring of new xylem was produced it was found that cutting off those shoots arrested totally the production of new xylem elements. However, the differentiation of the xylem initials was completed after 24 days, and the cambial zone returned to the pre-dormant condition (Fig. 6). Wodzicki (1965) postulated that the decreasing ratio of endogenous growth stimulators – auxins and gibberellins – to the endogenous inhibitors plays an important role in the differentiation of late wood in *Larix decidua* Mill. Recently Pieniążek and Rudnicki (1967) extracted and identified a powerful endogenous growth inhibitor – abscisic acid – from apple leaves and fruit. Abscisic acid is already identified (Milborrow 1967) as a main component of so called inhibitor- β (Kefford 1955). The availability of the inhibitor both synthetic and natural will help us to elucidate its role in the formation of summer wood in *Malus*.

The synthetic growth retardants such as CCC and B-9 failed to modify the production of cambial derivatives when used alone or in combination with auxin, cytokinin and gibberellin. The well known effects of growth retardants, especially B-9 on the restriction of growth of apple trees after spraying (Batter 1963; Modlibowska 1965) must be a result of the change in the production of endogenous growth regulators in the leaves. In case of leafless apple trees the growth retardants supplied directly to the stem did not seem to act as auxin or gibberellin antagonists in cambial activity and xylem differentiation.

The rate of cambial divisions induced by the interaction of NAA, BA and GA exceeded by far that found after 24 days in chilled control trees. It caused the splitting of the bark and the remarkable thickening of the stem (Fig. 4). This faster than normally occurring rate of cambial division might explain our failure in inducing normal wood differentiation with the mixture of three synthetic growth regulators (NAA, BA, GA).

In conclusion we would like to say that in *Malus* endogenous hormones, especially the auxins play the most important and key role in the initiation

of cambial activity and the differentiation of normal xylem components. Other factors such as cytokinins or gibberellins are needed to bring about the synergism in cambial divisions.

In the experiments such as ours with a mixture of synthetic growth regulators at least one of them had to be of endogenous origin to trigger normal differentiation of wood. Thus in disbudded chilled plants that were already producing in the roots endogenous regulators other than auxin the application of synthetic NAA to the decapitated stem induced in lower parts of apple seedlings normally differentiated layer of xylem. Also when only synthetic cytokinin (BA) was supplied to the dormant unchilled seedlings and the buds were stimulated into growth subsequently producing auxins and gibberellins the differentiation of very wide new growth increment resulted in almost normal wood (Fig. 13).

Additional support for this hypothesis is given by the production of xylem and bud growth induced by growth regulators in the older 4-year-old unchilled trees (Fig. 12). The treatment with NAA plus BA produced first a wide ring of abnormal wood, and then when the buds were stimulated into growth by BA present in the mixture of growth regulators a new layer of xylem was formed of remarkably normal appearance.

No specific role could be assigned for the time being to GA used alone. However gibberellic acid, the main component of Gibrescol used in our experiments, is known to exert very limited effect on apple trees (Barlow 1966). The effect of the endogenously produced gibberellins (GA_{4+7}), found by Dennis and Nitsch (1966) in apple seeds on bud growth and cambial activity are being investigated.

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SUMMARY

The effects of growth regulators α -naphthylacetic acid (NAA), benzyladenine (BA), Gibrescol (GA), 2-chloroethyl trimethylammonium chloride (CCC), N-dimethyl amino succinamic acid (B-9) and their mixtures - on the development of buds, cambial activity and the differentiation of new xylem in apple shoots were investigated. One-year-old 'Antonovka' seedlings and 4-year-old 'Antonovka' trees chilled and unchilled were used in the experiments. Growth regulators were supplied in water solution to the decapitated stems or petiole stumps (Fig. 1, 2).

NAA inhibited bud opening in chilled or unchilled trees after decapitation and

treatment with BA. GA stimulated the elongation of those buds that were previously stimulated into growth by wound effect or BA.

NAA reactivated the cambium in chilled and unchilled disbudded trees. Chilling is necessary only for buds. Developing buds produce then endogenous growth regulators, especially auxins that are essential for reactivation of the cambium.

NAA plus BA induces synergistically the rate of cambial divisions and as a result a wide ring of new xylem is formed. Meristematic activity in the parenchyma of the cortical layer is also greatly increased.

NAA plus GA produced similar synergistic effect on cambial divisions but the parenchymatous cells in the cortical layer are very little affected by this treatment.

The growth retardants (CCC and B-9) applied through the stem failed to modify the production of cambial derivatives when used singly or in combination with auxin, cytokinin and gibberellin.

New wood produced under the influence of NAA, NAA plus BA and NAA plus GA is abnormal. It was composed mostly of short vessels, parenchymatous cells and very few fiber-tracheids. Normal wood was produced only in these combinations of synthetic growth regulators where BA stimulated in unchilled trees the bud development, and in turn the buds produced endogenous auxins, or in chilled, disbudded trees when synthetic auxin was supplied at the time when the roots were already producing cytokinins.

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HORMONALNA REGULACJA AKTYWNOŚCI KAMBIUM I RÓŻNICOWANIA DREWNA W PĘDACH JABŁONI

Streszczenie

Badano wpływ regulatorów wzrostu takich jak kwas α -naftylooctowy (NAA), benzyloadenina (BA), Gibrescol (GA), chlorek chlorocholiny (CCC), kwas 1-N-dwumetyloaminobursztynowy (B-9) i mieszanin tych regulatorów na rozwój pąków, aktywność kambium i różnicowanie nowopowstałego drewna w pędach jabłoni. Materiałem doświadczalnym były jednoroczne siewki jabłoni i jednoroczne pędy drzewek 4-letnich odmiany 'Antonówka' po przechłodzeniu i bez przechłodzenia. Regulatory wzrostu podawano w roztworze wodnym do uciętych pędów lub przez ogonki liściowe (Rys. 1, 2).

NAA hamował rozwój pąków, który zachodził naturalnie u roślin po przechłodzeniu, względnie u roślin nieprzechłodzonych pod wpływem dekapitacji, czy też po potraktowaniu BA.

GA pobudzało wydłużanie pąków poprzednio pobudzonych do rozwoju przez dekapitację, czy też BA.

NAA wywoływał aktywność kambium u roślin przechłodzonych i nieprzechłodzonych po usunięciu z nich pąków. Przechłodzenie jest konieczne tylko dla pąków, które po rozwinięciu produkują endogenne regulatory wzrostu konieczne do pobudzenia kambium.

NAA plus BA wpływa wybitnie synergistycznie na szybkość podziałów komórek

kambium i powstaje szeroki pierścień nowego drewna. Następuje również bardzo silne powiększenie warstwy korowej.

NAA plus GA daje podobny efekt synergistyczny na podziały w kambium, ale nie wywołuje prawie żadnych zmian w warstwie korowej.

Retardanty wzrostu takie jak CCC i B-9 podane przez pędy nie wywołały żadnych uchwytynych zmian w aktywności kambium przy zastosowaniu ich zarówno pojedynczo, jak i z innymi regulatorami wzrostu.

Nowe drewno w kombinacjach NAA, NAA plus BA i NAA plus GA było nienormalne. Składało się ono przeważnie z krótkich naczyń, komórek parenchymatycznych i nielicznych cewek włóknistych. Drewno normalne można otrzymać jedynie w tych kombinacjach syntetycznych regulatorów wzrostu, kiedy pobudzone do rozwoju przez BA pąki u roślin nieprzechłodzonych wytworzyły endogenną auksynę lub u przechłodzonych roślin po wylupaniu pąków i po podaniu syntetycznej auksyny w tym momencie, kiedy korzenie dostarczyły już do pędu cytokininy.

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